RESEARCH ARTICLE

Post-fire succession of seeding treatments in relation to reference communities in the Great Basin

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Abstract

Questions: Post-fire seeding has been widely implemented in the semiarid Great Basin because natural vegetation recovery may be compromised. Non-native species are often seeded to rapidly establish perennial cover and compete with invasive annuals. We asked whether seeding treatments with different amounts of native and non-native species followed different successional trajectories and whether they became more similar to reference communities over time. We considered restoration implications of seed mix choices and reference community options involving: (a) local unburned vegetation; and (b) reference states mapped by the USDA Natural Resources Conservation Service (NRCS) based on soil–vegetation associations.

Location: Tintic Valley, UT, USA.

Methods: Four post-fire seeding treatments differing by seed mix were installed alongside an unseeded control (USC) at two sites. Two seed mixes were comprised of native species and two were predominantly non-native. Vegetation was monitored 1–3 and 16–18 years after fire and seeding. Reference communities were characterized and compared using hierarchical clustering. Non-metric multidimensional scaling and permutation tests were used to determine successional trajectories of post-fire treatments in relation to reference communities.

Results: Local unburned reference communities had fewer herbaceous perennials and higher woody cover than NRCS reference communities, suggesting departure from conditions expected under minimal post-settlement disturbance. USCs became more similar to reference communities over time, though less so at a site with abundant invasive annuals. Trajectories of seeded treatments were driven by seed mix species, with native-only mixes approaching reference communities more closely than mixes with non-natives.

Conclusions: Gradual recovery of reference community composition is possible without seeding but the degree and rate of recovery can vary by site. Seeding can accelerate perennial vegetation recovery but may result in alternative successional trajectories, especially if non-native species are seeded. Carefully selected reference communities can serve as guides for formulating seed mixes when restoration of natural vegetation is desired.

1 | INTRODUCTION

Human-mediated ecosystem alterations, such as introductions of invasive species, have the potential to disrupt natural successional processes following fire. Fire succession in dryland ecosystems of many regions has been impacted by invasions of non-native annual plants that can increase fire risk and lead to low-diversity annual communities perpetuated by repeated burning (D'Antonio & Vitousek, 1992; Chambers et al., 2019). In the semiarid Great Basin of western North America, risk of post-fire invasion by non-native annuals such as *Bromus tectorum* (Bradley et al., 2018; Mahood & Balch, 2019) is amplified by shifts in vegetation composition and structure that have occurred following the initiation of livestock grazing in the mid- to late 1800s (Pickford, 1932; Romme et al., 2009; Morris & Rowe, 2014). Areas that have experienced reductions of herbaceous perennials, often in combination with increased dominance of fire-intolerant woody plants, are likely to recover slowly following fire and thus provide an opening for annual invasion (Miller et al., 2013; Chambers et al., 2017; Urza et al., 2017). However, areas maintaining abundant native species capable of post-fire regeneration from seed or bud banks may be able to withstand competition from non-native annuals and follow successional trajectories toward native shrub-steppe or woodland communities (Miller et al., 2013; Ellsworth et al., 2016; Wainwright et al., 2020).

Seeding is a common management response to wildfire in the Great Basin and adjacent regions (Pilliod et al., 2017). Post-fire seeding efforts in the Great Basin have focused largely on short-term rehabilitation objectives such as stabilizing exposed soil and countering invasive annuals through rapid establishment of perennial cover (GAO, 2006; BLM, 2007). Non-native forage plants, mostly of Eurasian origin, have been widely used for rehabilitation seedings (Pilliod et al., 2017), although emphasis has increasingly been placed on seeding native species (Richards et al., 1998; Pilliod et al., 2017). Policy guidelines and strategies for US federal agencies emphasize the desirability of native species for wildlife habitat and ecosystem services (BLM, 2007; PCA, 2015; Olwell & Riibe, 2016). Seeding native species is likely to be particularly appropriate where short-term rehabilitation objectives are accompanied or superseded by a longer-term objective of restoring historical or pre-fire natural vegetation (BLM, 2007).

From a restoration perspective, seeding following fire or other disturbances is a strategy to assist or redirect succession toward a desired state (Sheley et al., 2006; Walker et al., 2010). Seeding may be unnecessary if the capacity for natural succession remains intact and the species driving the desired trajectory are still present in sufficient quantity (Holl & Aide, 2011; Walker et al., 2014). Otherwise, seeding native species adapted to the restoration site would presumably be the best option for accelerating succession toward a

natural vegetation target (Johnson et al., 2010). Alternatively, seeding non-native species might also ultimately lead to recovery of natural vegetation if the non-natives eventually die back, perhaps with management intervention, and allow for a transition to colonizing native species (D'Antonio & Meyerson, 2002). The latter argument has been made for easily established non-native species commonly seeded in the Great Basin, which could serve as competitors against undesirable invasives until later in succession when natives return (Cox & Anderson, 2004). However, this strategy carries the risk that non-native seeded species will persist and the transition to natives will fail to occur.

Restoration targets are often based on reference states assumed to indicate ecological characteristics prior to disturbance (Wortley et al., 2013; Walden & Lindborg, 2016). Reference states for plant community restoration are commonly drawn from minimally disturbed vegetation at or near a restoration site (e.g., Matthews & Spyreas, 2010). Although it may not be possible or desirable to exactly restore pre-disturbance communities, reference information can nevertheless be useful for planning restoration treatments and gauging their success (White & Walker, 1997; Monaco et al., 2012). Reference communities also represent possible outcomes of succession and are thus important for evaluating successional trajectories even outside of a restoration context (Prach et al., 2016). In many areas of the Great Basin, prospective reference communities are available at locations that have escaped burning over timespans corresponding to estimated natural fire return intervals of 35 to 300+ years (Baker, 2006; Romme et al., 2009; Bukowski & Baker, 2013). The suitability of these mid- to late-successional communities as restoration targets depends on the extent to which they deviate from desired conditions. Because of post-settlement impacts, many plant communities in the Great Basin are not considered entirely natural in the sense of representing a historical baseline (Romme et al., 2009; Morris & Rowe, 2014). In such settings, a natural reference state may need to be inferred from data gathered beyond the contemporary timeframe or immediate spatial vicinity of a site (White & Walker, 1997). Ecological site descriptions (ESDs) developed by the US Department of Agriculture, Natural Resources Conservation Service (NRCS) are a potential source of reference state information under these circumstances. ESDs contain characterizations of reference state plant communities for soil-based land classification units referred to as ecological sites (Caudle et al., 2013; NRCS, 2018b), typically with enough detail to be useful as a benchmark for evaluating species-level outcomes of restoration or succession.

In this study, we used monitoring data from a post-fire seeding experiment implemented at two sites in the eastern Great Basin to characterize plant community succession of treatments that included seed mixes containing predominantly non-native species, mixes with native species only, and an unseeded control (USC). We

asked whether these treatments followed different successional trajectories and whether they differed in degree of resemblance to reference communities during an 18-year timespan. Reference communities were defined using data from two sources, actual unburned vegetation (UB) at the study sites and mapped reference states from ESDs. Based on our understanding of the ecosystem, we anticipated that invasive non-native annuals would potentially impede succession toward reference communities in the absence of seeding, but that seeding might facilitate succession toward reference communities, especially if using native-only seed mixes. Our analysis included comparisons of the actual vs mapped reference communities and an assessment of their applicability as restoration targets.

2 | METHODS

2.1 | Study area

Post-fire seeding experiments were set up at two study sites, Mud Springs (ca. 1,780 m a.s.l.) and Jericho (ca. 1,660 m a.s.l.), both located on public lands in Tintic Valley, UT, that burned during the Railroad wildfire of July 1999 and have not reburned to date. Climate is continental and semiarid with mean temperatures of ca. 21°C in summer and ca. −2°C in winter (Wang et al., 2016, 2019). Precipitation fluctuates between years but is usually concentrated in the spring, fall, and winter (Appendix S1). During the timeframe of this study (1999–2017), mean annual precipitation was 350 mm at Mud Springs and 295 mm at Jericho (Wang et al., 2019). Soils are fine to very fine sandy loams with 1%–4% slopes at Jericho, and a mixture of cobbly, silty and sandy loams with 2%–8% slopes at Mud Springs (NRCS, 2018b). The sites are grazed on a rotational/seasonal basis by cattle at Mud Springs and sheep at Jericho (Bureau of Land Management, pers. comm.; Utah Land Trusts Administration, pers. comm.).

In November 1999, seeding treatments were installed to test four seed mixes differing in composition and proportions of native vs non-native species. Two "conventional" mixes predominantly containing species originating from Eurasia were developed by participants from two federal agencies, the US Department of Agriculture, Agricultural Research Service (ARS), and the US Department of the Interior, Bureau of Land Management (BLM). The other two mixes contained only native species (i.e., from western USA sources) and differed by seed mix diversity and seeding rates; the native low-diversity mix (NL) had fewer species and lower rates than the native high-diversity mix (NH; Table 1). Seeding rates were lower at Jericho, where seeding was carried out using rangeland drills, than at Mud Springs where seeding involved aerial broadcast followed by chaining (Table 1). At each site, the experiment was replicated in five blocks, each containing the four seeding treatments plus an USC in randomly-assigned rectangular strips (213 m × 73 m at Mud Springs, 213 m × 46 m at Jericho). Additional details about study sites, seeding treatments and seed mixes are presented in Thompson et al. (2006) and Ott et al. (2019).

2.2 | Data collection

Vegetation data were collected using methods adapted from the Utah Division of Wildlife Resources range trend studies (UDWR, 2019). The monitoring timespan lasted 18 years (2000–2017), although data collection occurred only during the first three post-fire growing seasons (2000, 2001, 2002) and three subsequent growing seasons beginning 16 years post-fire (2015, 2016, 2017). Measurements were taken from 20 quadrats 0.25 m^2 in area placed at 1.5-m intervals on each of 4–5 permanent transects per plot (3% of original quadrats at Mud Springs were discarded due to missing markers or atypical localized conditions, e.g., motor vehicle trails). Vascular plant species occurring in quadrats (rooted or overhanging) were identified and assigned using modified Daubenmire cover classes (≤1%, 1.1%–5%, 5.1%–15%, 15.1%–25%, 25.1%–50%, 50.1%–75%, 75.1%–95%, 95.1%–100%). Sampling was done late in the growing season when annual plants were senescent, from mid-July to early October with most sampling concentrated in August. Some quadrats were revisited at later dates to check questionable taxonomic identifications. Nomenclature follows USDA Plants (NRCS, 2018a).

Additional data were collected in 2017 from three UB areas located ca. 100–500 m from post-fire treatment blocks at each study site (Appendix S2). These areas occurred as patches within the 1999

TABLE 1 Seed mix diversity and bulk seeding rates of seed mixes applied at Mud Springs and Jericho study sites, UT, USA

Site	Seed mix	Number of species			Bulk seeding rate (kg/ha)		
		Native	Non-native	Total	Native	Non-native	Total
Mud Springs	ARS	6	5	11	9.5	14.2	23.7
	BLM	3	5	8	5.2	16.5	21.7
	NH	10	0	10	32.2	0	32.2
	NL	7	0	7	20.2	0	20.2
Jericho	ARS	4	5	9	3.7	7.1	10.8
	BLM	3	5	8	1.7	9.4	11.1
	NH	10	0	10	22.0	0	22.0
	NL	6	0	6	11.0	0	11.0

burn perimeter or just outside its margins. Although their fire history prior to 1999 is unknown, these areas exhibited characteristics of late-successional shrublands and woodlands of the region. Transects were installed in representative sections of these areas and data were collected from quadrats using the same methods as the post-fire treatments.

ESDs were obtained from the NRCS Web Soil Survey (NRCS, 2018b) for ecological sites that, according to soil map layers, occurred within 500 m of experimental blocks (Table 2; Appendix S2). Reference state plant community data were extracted from ESDs for each ecological site. All ESDs obtained in this way had provisional status and presented plant community data only for intermediate phases of reference states. Species listed for these ESD reference communities were all native, except for one presumably erroneous record of *Pennisetum purpureum*, which was removed from the data set prior to analysis.

2.3 | Data integration and analysis

Each combination of site, block, treatment and year from the post-fire seeding experiment was treated as a distinct community unit, along with each UB sample and ESD reference community. Percent cover was calculated for each species by averaging arithmetic midpoints of cover classes across quadrats within a unit. Percent cover was also calculated for growth form groups (annual and perennial forbs and grasses, shrubs, and trees) using a formula for aggregating cover class midpoints (Jennings et al., 2009, p. 185) wherever more than one member of a group was present in the same quadrat. Plants that could not be identified to species or genus were omitted from analyses, with the exception of wheatgrasses (*Agropyron* sensu lato) that were frequently indistinguishable in the field during the first three monitoring years. Omitted plants accounted for 0.1% of occurrences and 0.02% of cover values summed across all records.

Although the field methodology used to develop ESDs (Caudle et al., 2013) differed from our own, we were able to incorporate ESD data into our analyses by using community-scale species composition and abundance as a common currency between data sets. ESD reference community data, consisting of percent cover by group and annual production by species, were integrated with field data after being converted to percent cover by species. We assumed that annual production was approximately proportional to cover within groups and that total cover of a group could therefore be partitioned among species of the group according to their relative annual production. Because cover and annual production were presented as ranges in ESD reports, we used the midpoint between the upper and lower limits of the range in our calculations. When combining data sets, we sought to reduce variation due to closely related minor species by lumping them together. In other words, some of the "species" used in our analyses were actually comprised of multiple species within the same genus (e.g., *Astragalus* spp., *Erigeron* spp., *Lupinus* spp.).

Hierarchical clustering was used to evaluate compositional patterns among reference communities, and non-metric multidimensional scaling (NMDS) was used as an ordination technique to visualize patterns of community variation and identify successional trajectories of post-fire treatments in relation to reference communities for each site. Analyses were carried out in R (R Core Team, 2019) using the "hclust" function for clustering based on unweighted group averages and the "metaMDS" function from the *vegan* package (Oksanen et al., 2019) for NMDS. The Bray–Curtis coefficient with percent cover representing abundance was used as the measure of community dissimilarity in all cases. NMDS was implemented with 100 random iterations per run in 1–6 dimensions. Examination of stress values across dimensions showed that, for both sites, stress declined from the first through third dimension to ca. 0.15 and thereafter remained stable, indicating that three-dimensional solutions were optimal (McCune & Grace, 2002). To enhance interpretability, each NMDS ordination was rotated using the "MDSrotate" function (Oksanen et al., 2019) so that distances between post-fire treatments and ESD reference communities were maximized on the first axis.

We summarized community composition for each three-year period (2000–2002 = Period 1; 2015–2017 = Period 2) and carried out permutation tests to assess whether post-fire communities were becoming more similar to reference communities from one period to the next, and whether the degree of similarity differed between treatments. Similarities to UB and ESD reference communities were tested separately for each site, with the tested variable being the mean Bray–Curtis similarity (1 − Bray–Curtis dissimilarity) between a given post-fire community unit and the corresponding set of reference communities. We tested the statistical significance of differences between each pair of post-fire treatments within periods and between periods within treatments. Tests were carried out with the "pairwisePermutationTest" function in the *rcompanion* R package (Mangiafico, 2019), adapted to allow restricted permutations. The experiment's blocking structure was taken into account by restricting permutations within blocks, and for tests comparing treatments, permutations were also restricted within years. *p*-Values were adjusted for multiple comparisons using the false discovery rate of Benjamini and Hochberg (1995).

3 | RESULTS

3.1 | Community composition

3.1.1 | Reference communities

Hierarchical cluster analysis revealed three primary groupings of reference communities: ESD, UB at Mud Springs and UB at Jericho (Figure 1). ESD communities were drawn from nine ecological sites, five of which were mapped only at Mud Springs, one mapped only at Jericho, and three mapped at both locations (Table 2). The ecological sites were characterized by the NRCS as semidesert or upland

TABLE 2 Ecological sites (soil-based ecological units) occurring at the Mud Springs and Jericho study sites, UT, USA

Ecological Site Name	Mud Springs	Jericho
Semidesert Gravelly Loam (*Artemisia tridentata* ssp. *wyomingensis*) North	X	
Semidesert Loam (*Artemisia tridentata* ssp. *wyomingensis*)	X	X
Semidesert Sandy Loam (*Artemisia tridentata* ssp. *wyomingensis*)		X
Semidesert Shallow Hardpan (*Juniperus osteosperma*)	X	X
Upland Loam (*Artemisia tridentata* ssp. × *bonnevillensis*) North	X	
Upland Shallow Hardpan (*Pinus* spp.- *Juniperus osteosperma*)	X	
Upland Shallow Loam (*Artemisia nova*)	X	X
Upland Stony Loam (*Artemisia tridentata* ssp. *wyomingensis*)	X	
Upland Stony Loam (*Pinus* spp.-*Juniperus osteosperma*)	X	

X indicates that the ecological site occurred within 500 m of post-fire seeding treatments at a given study site, according to maps obtained from the USDA Natural Resources Conservation Service.

loams or hardpans with *Artemisia tridentata*, *Artemisia nova*, *Juniperus osteosperma* and/or *Pinus monophylla* as woody dominants (Table 2; Figure 1). Other woody species such as *Chrysothamnus viscidiflorus*, *Purshia tridentata*, and *Atriplex* spp. were also present in ESD, alongside co-dominant perennial grasses including *Pseudoroegneria spicata*, *Achnatherum hymenoides*, *Poa secunda*, *Elymus elymoides*, and *Hesperostipa comata* (Tables 3, 4; Figure 1). In total, over 75 species were listed for ESD communities, all of which were perennial (Appendixes S3, S4). UB communities had greater dominance of woody species and lower diversity and abundance of herbaceous perennials compared to ESD (Tables 3, 4; Figure 1; Appendixes S3, S4). UB at Jericho, with ca. 20 recorded species (Appendix S4), was dominated by *Artemisia tridentata*, with lesser amounts of *Chrysothamnus viscidiflorus* and widely scattered *Juniperus osteosperma* (Figure 1). The only herbaceous species with >1% cover in UB at Jericho was the non-native annual grass *Bromus tectorum* (Figure 1). UB at Mud Springs had ca. 40 species (Appendix S3) and was dominated to varying degrees by *Juniperus osteosperma* and *Pinus monophylla* with an understorey that was either sparse, dominated by *Artemisia tridentata*, or co-dominated by *Artemisia tridentata* and *Pseudoroegneria spicata* (Figure 1).

3.1.2 | Post-fire treatments

Of the more than 120 species recorded in post-fire treatments over the course of the study (Appendixes S3, S4), 27 species had a mean cover ≥1% in at least one community unit (Tables 3, 4), and these species accounted for approximately 90% of total plant cover.

Annuals were most abundant in USC, especially at Jericho, and were dominated by the non-native annual grass *Bromus tectorum*, non-native annual forbs including *Alyssum desertorum*, *Salsola tragus* and *Sisymbrium altissimum* (Tables 3, 4), and to a lesser extent native annual forbs such as *Gilia* spp., *Descurainia pinnata* and *Nicotiana attenuata* (Appendixes S3, S4). Cover in seeded treatments (ARS, BLM, NH, NL) became dominated by species that had been part of the seed mixes, including non-native perennial grasses (e.g., *Agropyron* spp., *Thinopyrum intermedium*, *Bromus inermis*), native perennial grasses (e.g., *Pascopyrum smithii*, *Pseudoroegneria spicata*, *Hesperostipa comata*), and native shrubs (e.g., *Artemisia tridentata*, *Atriplex canescens*; Tables 3, 4). Perennials in USC were predominantly native and included seed mix species that were either already present from residual populations or entered as a result of seeding treatments. At Mud Springs, cover of non-seeded native shrubs such as *Ericameria nauseosa*, *Chrysothamnus viscidiflorus*, and *Gutierrezia sarothrae* was higher in USC than seeded treatments (Table 3; Appendix S3). At Jericho, few perennials became established in USC besides the non-seeded native shrub *Ericameria nauseosa* (Table 4; Appendix S4).

3.2 | Axes of community variation and post-fire trajectories

NMDS ordinations showed that communities at Mud Springs and Jericho were structured along similar axes of variation (Figures 2, 3). Due to axis rotation, ESD reference communities were positioned at the right side of Axis 1 for both sites, and the most important patterns were visible in plots of Axes 1 vs 2 and 3 (Figures 2, 3). UB reference communities were located close to ESD on Axis 1 with post-fire treatments (ARS, BLM, NH, NL, USC) farther to the left (Figures 2, 3). Cover of shrubs and trees was positively correlated with Axis 1 (Figures 2a,b, 3a,b), reflecting a greater abundance of woody plants in ESD and UB. Perennial grass cover was positively correlated with Axis 2, while annual forb cover was negatively correlated (Figures 2a, 3a). Cover of annual grasses and annual forbs was positively correlated with Axis 3 (Figures 2b, 3b).

At Mud Springs, successional trajectories of post-fire treatments progressed along Axis 2 (indicating increasing perennial grass cover) each succeeding year until 2015, after which there was modest retreat along that axis (Figure 2c). ARS and BLM were closely aligned in a near-vertical trajectory along Axis 2, with little movement along Axis 1, while NL and NH were aligned in a diagonal trajectory that brought them closer to ESD (Figure 2c). USC initially followed a trajectory aligned with NL and NH but veered away in 2015–2017 and ultimately did not progress as far as other treatments on Axes 1 and 2 (Figure 2c). On Axis 3, USC moved farther than other treatments due to higher annual grass cover (Figure 2d). UB was positioned opposite USC on Axis 3, with low cover of annual grasses but high tree cover (Figure 2d).

At Jericho, all post-fire treatments followed successional trajectories toward higher perennial grass cover on Axis 2 (peaking in 2015 or 2016) while diverging along Axis 1 (Figure 3c). By 2015–2017, NH
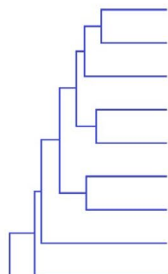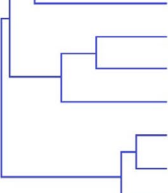
	Annual Grass	Perennial Grasses									Shrubs								Trees	
	BRTE	ACHY	ELEL	HECO	KOMA	PASM	PLJA	POFE	POSE	PSSP	ARNO	ARTR	ATCA	ATCO	CHVI	KRLA	PUST	PUTR	JUOS	PIMO
ESD Upland Loam (ARTRB) North		6	2	1	1	1			4	9		5	1		1			1		
ESD Semidesert Loam (ARTRW)		7	2	2		2	2		2	9	1	7	1	1	1	1				
ESD Semidesert Gravelly Loam (ARTRW) North		4	2	1		1			1	13	1	14		4	2	1				
ESD Upland Stony Loam (ARTRW)		2	2	1	2	1	1	2	2	12	1	7			1			3		
ESD Upland Stony Loam (Pinus-JUOS)		2	1	1	1	1	1	2	1	6	3	6	1		1		1	5	2	6
ESD Upland Shallow Hardpan (Pinus-JUOS)		5	2	2	1	1			1	5	8	3		1	1		3	3	4	11
ESD Semidesert Shallow Hardpan (JUOS)		7	2	3			1		1	7	8	1		1	1	2	1		8	
ESD Upland Shallow Loam (ARNO)		1		1					4	17	19				2			1		
ESD Semidesert Sandy Loam (ARTRW)		13	2	6		2	2					3	3	1	2	3				
UB Mud Springs Block 3	0	0	0	0		0			1	5		3							13	1
UB Mud Springs Block 1	0	0	1	0		1			1			11			0				14	
UB Mud Springs Block 5	0	0	1						0						0			1	27	8
UB Jericho Block 4	4		0									18			0				1	
UB Jericho Block 2	3	0	0	0								20				5			0	
UB Jericho Block 5	1		0			0						23								

FIGURE 1 Reference communities for study sites in Tintic Valley, UT, arranged by compositional similarity through hierarchical clustering. Unburned communities (UB) were sampled from late-successional vegetation near post-fire treatments at the two sites (Mud Springs and Jericho). Ecological site description (ESD) communities were mapped at one or both sites by the US Natural Resources Conservation Service. Mean percent cover values are shown for species with ≥2% cover in at least one community; blank cells indicate absence. Species abbreviations: ACHY, *Achnatherum hymenoides*; ARNO, *Artemisia nova*; ARTR, *Artemisia tridentata* (ARTRB, ssp. ×*bonnevillensis*; ARTRW, ssp. *wyomingensis*); ATCA, *Atriplex canescens*; ATCO, *Atriplex confertifolia*; BRTE, *Bromus tectorum*; CHVI, *Chrysothamnus viscidiflorus*; ELEL, *Elymus elymoides*; HECO, *Hesperostipa comata*; JUOS, *Juniperus osteosperma*; KOMA, *Koeleria macrantha*; KRLA, *Krascheninnikovia lanata*; PASM, *Pascopyrum smithii*; PIMO, *Pinus monophylla*; PLJA, *Pleuraphis jamesii*; POFE, *Poa fendleriana*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*; PUST, *Purshia stansburiana*; PUTR, *Purshia tridentata*. All species shown are native except for BRTE

was situated closest to ESD on Axis 1, followed by NL, USC, ARS and BLM (Figure 3c). Trajectories along Axis 3 at Jericho led to the segregation of USC at one end (aligned with higher annual grass cover), ARS/BLM at the opposite end, and NH/NL in an intermediate position (Figure 3d). Unlike Mud Springs, Axis 3 at Jericho was unrelated to tree cover and UB communities were broadly distributed along its length (Figure 3b).

3.3 | Similarity of post-fire treatments to reference communities

Mean Bray–Curtis similarity of post-fire treatments to ESD and UB reference communities (here abbreviated sim-ESD and sim-UB, respectively) ranged from 0.01 to 0.29 (on a scale from 0 = complete dissimilarity to 1 = complete similarity) across tested treatments, periods, and sites (Figure 4). Differences between treatments generally became more pronounced between Periods 1 and 2 (Figure 4). The most notable changes between periods involved sim-ESD increases of ca. 0.1 in the NH, NL and USC treatments at Mud Springs (Figure 4b). Similarity values also increased for sim-ESD in NL and USC at Jericho (Figure 4d), sim-UB in NH and USC at Mud Springs (Figure 4a) and sim-UB in NL and USC at Jericho (Figure 4c). There were no cases of increasing similarity to either reference community type for ARS or BLM at either site; consequently, sim-UB and

sim-ESD values of ARS and BLM were significantly lower than other treatments by Period 2 (Figure 4). Sim-UB and sim-ESD were, in most instances, highest in NH, followed by NL and USC, although differences between these three treatments were not always significant (Figure 4). Sim-UB at Jericho was driven primarily by shared *Bromus tectorum* rather than the shared native species that influenced similarity values in other instances.

4 | DISCUSSION

4.1 | Reference communities and restoration targets

Reference communities obtained from ESDs did not resemble unburned communities sampled at the study sites closely enough to be considered interchangeable. ESD and UB both featured characteristic fire-intolerant woody species but differed in overall community composition and diversity. ESD had lower abundance of woody species, higher abundance of herbaceous perennials, more native species and fewer (zero) non-native species compared to UB. These differences can be partly attributed to differences in sampling procedures and measurements employed in two distinct data collection efforts. ESD reference communities mapped for our study site were apparently based on sample locations with local floras that differed from

TABLE 3 Mean percent cover of dominant species in reference communities and post-fire seeding treatments during two periods (2000–2002 and 2015–2017) at Mud Springs study site, UT, USA

	Period 1 (2000–2002)					Period 2 (2015–2017)					Reference	
	ARS[a]	BLM	NH	NL	USC	ARS	BLM	NH	NL	USC	UB	ESD
Annual Grasses												
Bromus tectorum[b]	0.2	0.1	0.1	0.1	0.3	0.4	0.4	1.3	1.0	4.4	0.1	–
Annual Forbs												
Alyssum desertorum[b]	3.6	2.3	4.1	4.2	6.7	0.4	0.3	0.5	0.5	1.2	0.5	–
Perennial Grasses												
Achnatherum hymenoides	0.9	0.7	1.3	1.5	0.7	0.6	0.5	1.3	1.5	1.8	0.1	4.3
Agropyron cristatum[b,c]	4.2	3.6	0.2	0.2	+	11.6	7.7	0.6	0.3	1.1	+	–
Bromus inermis[b]	0.3	1.6	0.2	0.1	–	0.7	5.5	0.8	1.0	0.3	–	–
Elymus elymoides	0.2	0.2	0.3	0.3	0.4	+	+	0.4	0.5	1.3	0.4	1.5
Hesperostipa comata	+	+	0.2	0.1	+	0.2	0.2	0.6	0.4	1.0	0.1	1.4
Leymus cinereus	+	–	0.2	–	–	0.1	0.2	2.9	+	+	–	0.1
Pascopyrum smithii	1.4	1.2	2.2	2.0	2.0	4.2	1.7	7.4	10.7	2.9	0.3	0.8
Poa secunda	0.4	0.3	0.4	0.4	0.4	0.3	0.4	0.5	0.4	0.9	0.9	1.8
Psathyrostachys juncea[b]	0.3	0.3	0.1	+	–	1.2	0.7	+	0.1	+	–	–
Pseudoroegneria spicata[d]	0.6	0.7	2.5	3.2	+	0.4	1.2	5.5	6.2	0.2	1.5	9.8
Thinopyrum intermedium[b]	0.1	1.2	0.1	0.1	–	0.4	1.5	+	0.2	0.5	–	–
Thinopyrum ponticum[b]	0.1	0.9	0.2	+	0.1	0.1	1.2	+	–	+	–	–
Shrubs												
Artemisia nova	–	–	–	–	–	–	–	–	–	–	–	5.0
Artemisia tridentata	–	–	0.1	+	+	–	–	2.1	0.5	1.3	4.5	5.3
Chrysothamnus viscidiflorus	+	+	+	+	+	0.2	+	0.2	0.2	3.7	0.1	1.3
Ericameria nauseosa	–	+	–	–	–	0.5	0.2	0.1	1.7	4.2	–	0.1
Gutierrezia sarothrae	+	0.1	+	+	0.2	0.1	0.2	0.4	0.4	1.9	0.3	0.6
Purshia tridentata	+	+	+	+	–	–	+	+	–	–	0.3	1.6
Trees												
Juniperus osteosperma	+	–	–	+	–	0.2	–	–	–	–	18.1	1.6
Pinus monophylla	–	–	–	+	–	–	–	–	–	–	2.9	2.1

Only species with mean cover ≥1% in at least one instance are shown (see Appendix S3 for full species table). – indicates zero recorded cover; +indicates mean cover <0.1%; shading indicates seeded species for given treatment.

[a]Post-fire treatments and reference communities: ARS indicates Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, native high-diversity mix; NL, native low-diversity mix; USC, unseeded control; UB, local unburned reference; ESD, ecological site description reference.

[b]Non-native species.

[c]Includes *Agropyron desertorum* which was not differentiated from *Agropyron cristatum* during field sampling.

[d]Includes *Elymus wawawaiensis* which was not differentiated from *Pseudoroegneria spicata* during field sampling.

those we encountered. We attempted to compensate for fine-scale floristic variation by relaxing species identity and lumping closely related species for analysis. We also took a relaxed approach regarding ESD selection (selecting all ecological sites that had been mapped within 500 m of treatment blocks) to broaden the pool of reference communities and compensate for potential fuzziness of ecological site boundaries, although this approach may have resulted in inclusion of ESDs that were not truly applicable to the treated areas. We did not formally verify the accuracy of ecological site mappings, but suspect a mapping error in the case of *Artemisia nova* communities which we did not detect in the vicinity of the study sites. While such data discrepancies contributed to differences between ESD and UB,

TABLE 4 Mean percent cover of dominant species in reference communities and post-fire seeding treatments during two periods (2000–2002 and 2015–2017) at Jericho study site, UT, USA

	Period 1 (2000–2002)					Period 2 (2015–2017)					Reference	
	ARS[a]	BLM	NH	NL	USC	ARS	BLM	NH	NL	USC	UB	ESD
Annual grasses												
Bromus tectorum[b]	1.7	1.1	1.5	2.4	2.0	2.0	1.8	5.9	6.2	13.9	2.7	–
Annual forbs												
Alyssum desertorum[b]	4.9	4.1	4.4	4.1	6.3	0.3	0.3	0.8	0.8	0.9	0.5	–
Erodium cicutarium[b]	–	–	–	–	–	+	+	0.1	0.5	1.5	–	–
Gilia spp.	1.9	2.1	2.0	2.2	1.7	+	+	+	+	+	0.1	–
Salsola tragus[b]	7.8	6.5	6.2	9.3	12.1	0.1	0.4	0.2	1.2	3.4	–	–
Sisymbrium altissimum[b]	0.2	0.1	0.3	0.4	0.5	0.2	0.2	0.2	0.4	1.1	+	–
Perennial grasses												
Achnatherum hymenoides	0.8	+	3.8	1.1	+	+	0.1	0.3	0.1	0.5	+	7.0
Agropyron cristatum[b,c]	2.8	2.0	0.1	0.1	+	15.4	5.0	0.3	1.4	0.6	+	–
Elymus elymoides	0.2	0.2	0.1	0.1	0.1	0.1	+	0.1	0.7	0.9	0.2	1.3
Hesperostipa comata	+	–	0.2	+	+	+	+	2.1	0.7	0.9	+	3.0
Leymus cinereus	+	–	+	+	–	+	+	1.0	–	–	–	–
Pascopyrum smithii	0.2	0.3	0.6	0.2	+	3.5	0.7	10.3	8.9	+	+	0.9
Pleuraphis jamesii	–	–	–	–	–	–	–	–	–	–	–	1.1
Poa secunda	+	+	0.1	+	+	–	–	+	+	+	–	1.5
Pseudoroegneria spicata[d]	0.2	0.2	1.2	0.6	+	+	–	1.2	0.6	–	–	8.3
Thinopyrum intermedium[b]	+	0.8	+	+	–	+	8.7	+	0.2	0.3	–	–
Thinopyrum ponticum[b]	+	1.6	0.1	0.1	–	–	0.6	–	–	–	–	–
Perennial forbs												
Medicago sativa[b]	1.1	0.5	+	0.2	+	–	–	–	+	–	–	–
Shrubs												
Artemisia nova	–	–	–	–	–	–	–	–	–	–	–	7.0
Artemisia tridentata	–	–	+	+	–	–	–	0.1	–	–	20.4	2.6
Atriplex canescens	+	+	0.1	0.1	–	–	0.1	2.7	0.6	–	–	1.0
Chrysothamnus viscidiflorus	–	–	+	–	–	–	–	–	+	+	1.6	1.6
Ephedra spp.	–	–	–	–	–	–	–	–	–	–	–	1.1
Ericameria nauseosa	–	–	+	–	–	0.5	0.2	0.2	1.3	1.6	–	–
Krascheninnikovia lanata	–	–	–	–	–	–	–	–	–	–	–	1.6
Trees												
Juniperus osteosperma	–	–	–	–	–	–	–	–	–	–	0.3	1.9

Only species with mean cover ≥1% in at least one instance are shown (see Appendix S4 for full species table). −indicates zero recorded cover; +indicates mean cover <0.1%; shading indicates seeded species for given treatment.

[a]Post-fire treatments and reference communities: ARS indicates Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, native high-diversity mix; NL, native low-diversity mix; USC, unseeded control; UB, local unburned reference; ESD, ecological site description reference.

[b]Non-native species.

[c]Includes *Agropyron desertorum* which was not differentiated from *Agropyron cristatum* during field sampling.

[d]Includes *Elymus wawawaiensis* which was not differentiated from *Pseudoroegneria spicata* during field sampling.
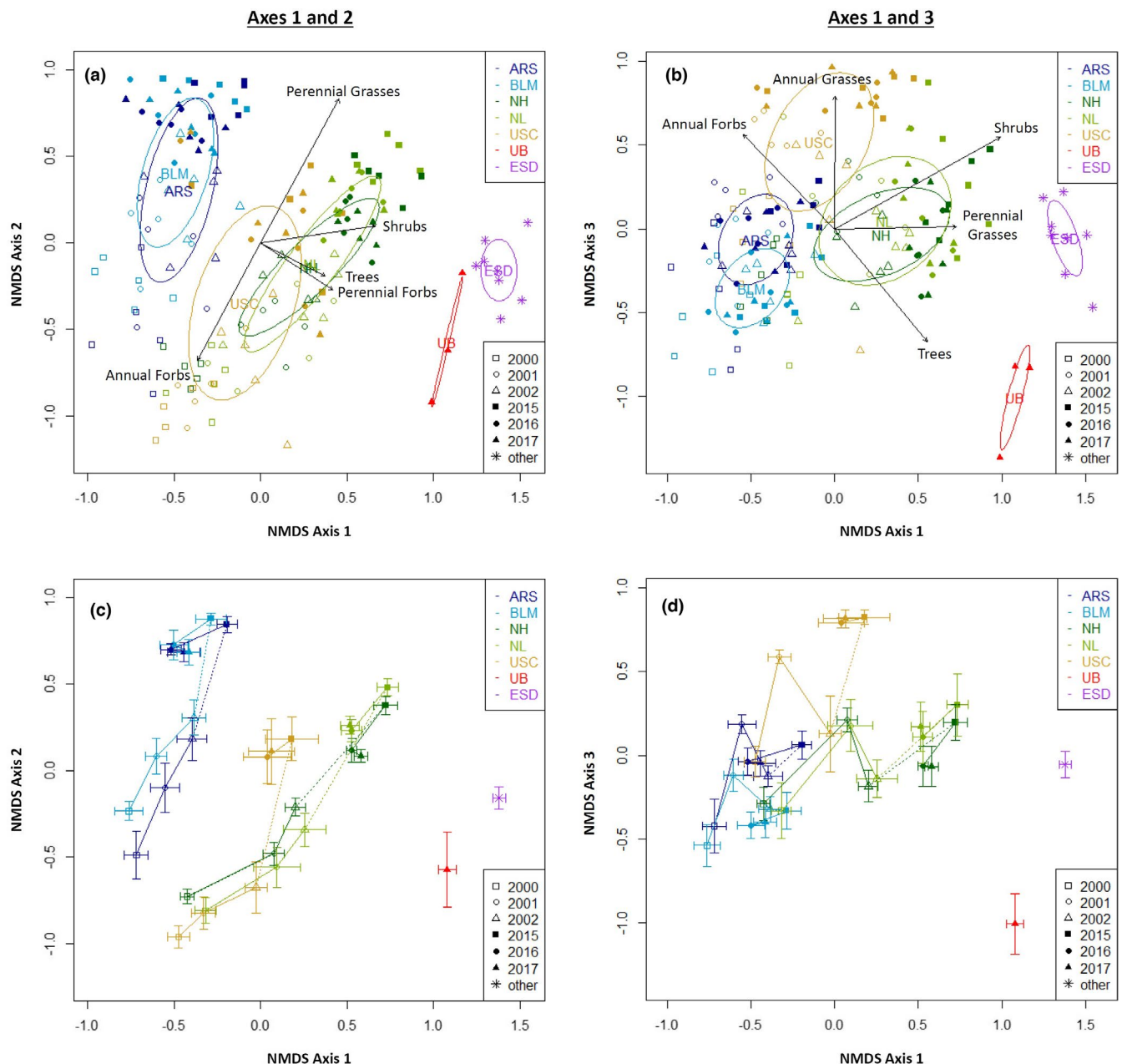
FIGURE 2   Ordination of plant communities at the Mud Springs aerial-seeded site in Tintic Valley, UT, showing trajectories of post-fire treatments (ARS, BLM, NH, NL, USC) over time following a 1999 wildfire, in relation to reference communities based on local unburned areas (UB) and ecological site descriptions (ESD). Distances between ESD and post-fire treatments are maximized on Axis 1. (a,b) Points represent individual units (defined by block, treatment and year), ellipses show standard deviations around treatment centroids, and vectors show strength and direction of significant ($p < 0.05$) correlations with growth forms. (c,d) Points are treatment/year centroids, bars are standard errors in the *x* and *y* dimensions, and lines connect centroids of sequential years within treatments. ARS, Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, native high-diversity mix; NL, native low-diversity mix; USC, unseeded control

perhaps the most significant reason for reference community differences is that ESD communities represent mid-successional community phases with minimal post-settlement human impacts, while UB communities appear to be later successional phases that have been subjected to post-settlement disturbances such as livestock grazing and non-native species invasions.

Woody species are known to become increasingly dominant in late-successional phases of Great Basin shrublands and woodlands,

typically accompanied by a decline in the herbaceous understorey (Barney & Frischknecht, 1974; Miller et al., 2000; Roundy et al., 2014). This can occur even in the absence of livestock (Ellsworth et al., 2016) but is likely to be more accelerated and severe where livestock grazing contributes to understorey removal (Pickford, 1932; Morris & Rowe, 2014). UB communities at Jericho showed signs of grazing impacts, and it is reasonable to assume that they have been heavily grazed given their proximity to a former
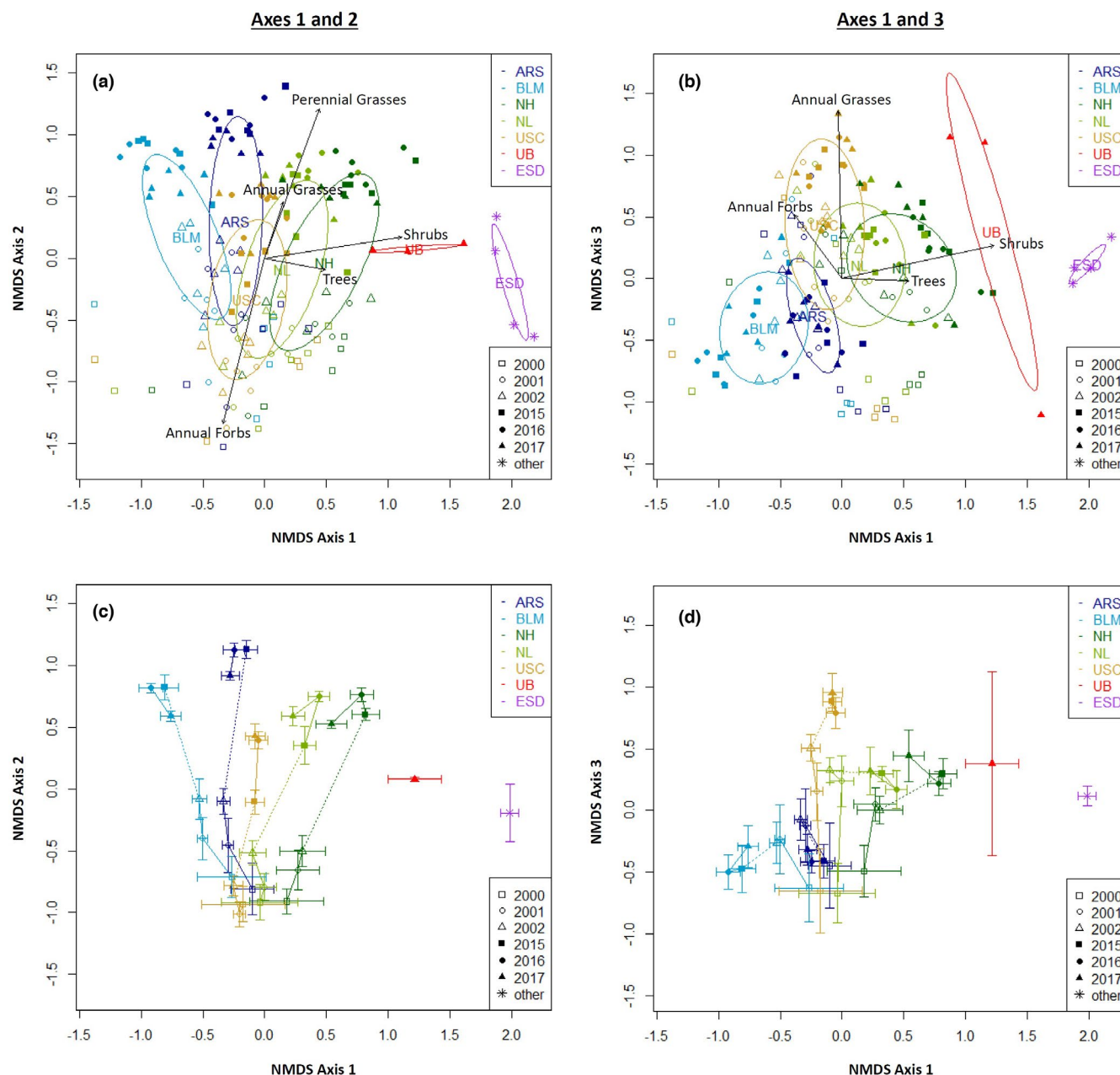
FIGURE 3 Ordination of plant communities at the Jericho drill-seeded site in Tintic Valley, UT, showing trajectories of post-fire treatments (ARS, BLM, NH, NL, USC) over time following a 1999 wildfire, in relation to reference communities based on local unburned areas (UB) and ecological site descriptions (ESD). Distances between ESD and post-fire treatments are maximized on Axis 1. (a,b) Points represent individual units (defined by block, treatment and year), ellipses show standard deviations around treatment centroids, and vectors show strength and direction of significant ($p < 0.05$) correlations with growth forms. (c,d) Points are treatment/year centroids, bars are standard errors in x and y dimensions, and lines connect centroids of sequential years within treatments. ARS, Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, native high-diversity mix; NL, native low-diversity mix; USC, unseeded control

sheep corralling station (Van Cott, 1991). Current grazing levels are lower than they were in the early 20th century (Longmore & Forrest, 2016), but effects of past heavy grazing can persist for decades (Courtois et al., 2004; Yeo, 2005). Mud Springs appeared to have been less heavily impacted by grazing than Jericho but had greater cover of dryland conifers (*Juniperus osteosperma* and *Pinus monophylla*). Expansion or infilling of these conifers at previously shrub-dominated sites has occurred throughout the Great Basin

and has often been attributed to grazing, although natural succession aided by fire suppression and CO_2 enrichment may have also contributed (Romme et al., 2009).

Differing characteristics of UB and ESD reference communities point toward different uses in research and restoration contexts. As examples of actual late-successional vegetation, UB communities can be viewed as null expected outcomes of succession given conditions that have prevailed in the recent past. However, because of
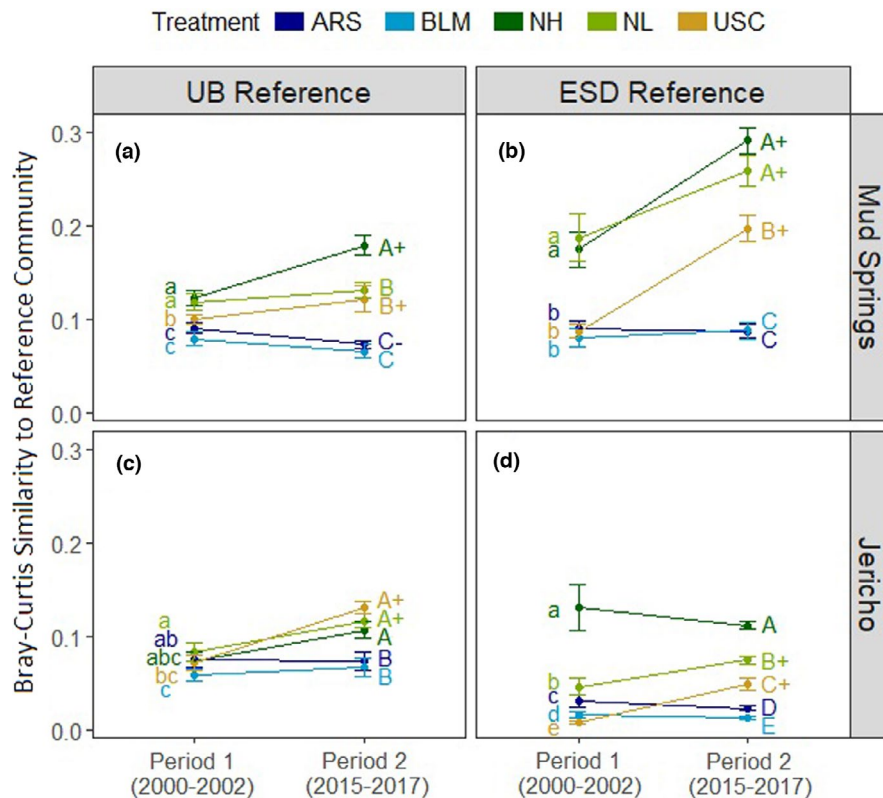
FIGURE 4 Bray–Curtis similarity of post-fire treatments in relation to reference communities based on local unburned areas (UB) and ecological site descriptions (ESD), during two time periods at two sites (Mud Springs and Jericho) in Tintic Valley, UT, USA. Points and error bars are means and standard errors for each combination of treatment (colors), period (X-axes), site (horizontal panels) and reference community (vertical panels); higher values along Y-axes indicate greater similarity of treatments to indicated reference communities. In each panel, different letters indicate significant ($p < 0.05$) differences between treatments within periods, i.e., lowercase letters for Period 1 (2000–2002, corresponding to post-fire years 1–3) and uppercase letters for Period 2 (2015–2017, or post-fire years 16–18). Significant ($p < 0.05$) increases and decreases from Period 1 to 2 are shown by + and − symbols, respectively. ARS, Agricultural Research Service mix; BLM, Bureau of Land Management mix; NH, native high-diversity mix; NL, native low-diversity mix; USC, unseeded control

their departure from the natural baseline (conditions prior to Euro-American settlement), limited diversity, and an overabundance of woody species, the UB communities we sampled would likely not be favored as restoration targets under prevailing paradigms of restoration and land management in the Great Basin. ESD reference communities, particularly those based on mid-successional phases with a balance of woody and herbaceous components, would likely be viewed as more desirable targets than UB across a range of management objectives, from restoring natural vegetation to maintaining forage, wildlife habitat and watershed resources (Floyd & Romme, 2012; Roundy et al., 2014; Summers & Roundy, 2018; Reinhardt et al., 2020). Our analyses demonstrate that ESD data can be directly integrated into quantitative assessments of restoration success when ESD reference states are desired targets.

4.2 | Post-fire succession across seeded and unseeded treatments

We found that plant communities changed during a post-fire interval comprised of two three-year monitoring periods (years 1–3

and 16–18) and that successional trajectories were influenced by seeding. Change was evident at both study sites, both within monitoring periods and between them. Directional changes during years 1–3 were consistent with observations of early post-fire succession elsewhere in the semiarid Great Basin, where colonizing or resprouting plants can rapidly occupy bare soil exposed by fire (e.g., Bates et al., 2020; Ott et al., 2001; Urza et al., 2017). Further changes occurred between years 3 and 16 as annual forbs declined, annual grasses expanded, and perennials increased in cover, similar to patterns reported in other studies spanning the same post-fire timeframe (e.g., West & Yorks, 2002; Chambers et al., 2014; Bates et al., 2020). Although we expected the pace of successional change to have slowed by the end of our monitoring timeframe, we noted inter-annual shifts in community composition during years 16–18, primarily driven by diminishing perennial grass cover. These shifts may have been caused by variation in weather conditions, grazing disturbance, or measurement bias of field crews in different years. Inter-annual shifts in years 16–18 did not reverse the overall pattern of change between periods, but they suggest that succession in this system is not strictly directional and that rapid changes can occur beyond the initial post-fire phase (West & Yorks, 2002).

The primary effect of seeding was to increase perennial grass cover and reduce cover of invasive annuals, as previously reported by Ott et al. (2019). This was true for all seed mixes, but more so for mixes with non-native species. Not all seeded grasses were equally successful or persistent, but enough of them reached high abundance to make a lasting mark on plant community composition. Long-term persistence was presumably the intent of the seeding treatments of the current study, in contrast to seedings utilizing short-lived species such as sterile ryegrass (Waitman et al., 2009) or potentially native annual forbs (Leger et al., 2014) as transient early-successional placeholders.

Without seeding, post-fire succession in the semiarid Great Basin is likely to be driven by the relative availability of propagules of native perennials and non-native annuals and the relative favorability of post-fire conditions for these competing groups (Chambers et al., 2014, 2019; Ellsworth et al., 2016; Bates et al., 2020; Wainwright et al., 2020). The two study sites showed contrasting responses related to these factors. At Mud Springs, native perennials readily recolonized the unseeded burns from residual buds or seeds, limiting the amount of annual invasion and leading to relatively high similarity between USC and reference communities, especially ESD. This response appears to be partly due to seed drift and colonization from adjacent seeded treatments, but it also suggests that natural successional processes remained intact at Mud Springs. At Jericho, the scarcity of residual perennials combined with favorable conditions for growth of invasive annuals resulted in annual dominance and low resemblance of USC to both ESD and UB. There is a possibility that, given sufficient time and the right combination of conditions, an annual-dominated community such as USC at Jericho could transition toward a later-successional state (Hanna & Fulgham, 2015; Morris & Leger, 2016), but the typical expectation is that it will persist with limited potential for successional change, particularly because of the risk of recurring fire (Knapp, 1996; Mahood & Balch, 2019).

4.3 | Effects of seed mixes on post-fire succession

Our expectation that seeding native species would facilitate succession toward reference communities was met to a degree. Compared to USC, native-only seed mix treatments (NH, NL) were more similar to ESD reference communities and were equally or more similar to UB across monitoring periods. Similarity of NH and NL to reference communities increased over time in the majority of cases and by Period 2 was generally highest for NH, the mix with the highest diversity and highest seeding rates. At Mud Springs in particular, post-fire conditions were favorable for establishment and persistence of seeded species that were important reference community components, e.g., *Pseudoroegneria spicata*, *Achnatherum hymenoides* and *Artemisia tridentata*. Cover of *Artemisia tridentata* in NH at Mud Springs was nearly halfway to reference community levels by Period 2, indicating more rapid post-fire recovery than typically observed for this species (Barney & Frischknecht, 1974; Shriver et al., 2019;

Bates et al., 2020). However, there was still considerable dissimilarity between native-only seeding treatments and reference communities, much of it due to non-matching proportions of common species. For example, native-only seedings had higher abundance of the grass *Pascopyrum smithii* than ESD at both sites, and at Jericho, *Atriplex canescens* had higher cover in native-only seedings than the normally dominant shrub *Artemisia tridentata*. Many less common species also failed to match up, including native perennial forbs that were recorded in ESD but absent from native-only seedings. Presumably, higher similarity could have been attained if seed mix composition had been formulated to more closely match reference community composition, using plant materials well adapted to site conditions but not more aggressive than naturally-occurring populations (Poelman et al., 2019).

Seeding treatments using conventional seed mixes (ARS, BLM) did not become more similar to reference communities but followed an alternative successional trajectory with increasing dominance by non-native seeded grasses. This outcome is not surprising since the ARS and BLM seed mixes included non-native grasses such as *Agropyron cristatum*, *Thinopyrum intermedium* and *Bromus inermis* that are known to be competitive and persistent in many areas where they have been seeded (Hull & Klomp, 1966; Allen-Diaz & Bartolome, 1998; Walker, 1999). Some stands of *Agropyron cristatum* have been found to persist with minimal recruitment of native plants for multiple decades (Hull & Klomp, 1966; Allen-Diaz & Bartolome, 1998), although in other cases, native species such as *Artemisia tridentata* have gained a foothold over time (Nafus et al., 2016; Williams et al., 2017; Davies et al., 2020), or co-planted native grasses have been able to maintain their presence (Nafus et al., 2015; Hamerlynck & Davies, 2019; Stonecipher et al., 2019). The success of native plants in non-native grass stands is likely to be greatest at locations where the non-natives are marginally adapted, have low initial establishment or are selectively reduced by factors such as grazing (Walker, 1999; Nafus et al., 2016, 2020; Williams et al., 2017); otherwise, native plant diversity and abundance can be limited by non-native grass competition (Walker, 1999; Scasta et al., 2015; Williams et al., 2017; Copeland et al., 2019; Stotz et al., 2019). Non-native seeded grasses of the ARS and BLM mixes appeared to be well adapted to conditions at our study sites and would not be expected to transition to a native community without intensive intervention, likely requiring costly mechanical or chemical control and additional seeding treatments (Hulet et al., 2010; McAdoo et al., 2017; Morris et al., 2019).

5 | CONCLUSION

This study presented an analysis of post-fire successional development over 18 years at two Great Basin sites where seeding treatments were installed in an operational-scale experiment. While limited in spatial extent, the sites can be placed in the broader context of Great Basin environments based on their different levels of resistance to annual invasion and resilience to fire disturbance

(Chambers et al., 2014, 2019). The Mud Springs site possessed these attributes to an extent that arguably lessened the need for seeding, while Jericho exemplified a setting with low resistance and resilience where seeding was more crucial. The contrasting post-fire responses of these two sites illustrate the importance of carefully evaluating site recovery potential when developing restoration prescriptions.

Due to their diminished "naturalness", we concluded that local unburned reference communities were not ideal restoration targets, though they served as null expected outcomes of succession in our assessment. Reference communities described in ESDs provided a more solid, though not perfect, basis for defining natural vegetation states. We conclude that ESDs are a valuable resource for this purpose, especially as they become finalized and add species cover values to their output (Caudle et al., 2013). More generally, our observations underscore the importance of seeking reference community data that best fit their intended use, and not assuming that existing communities closest to a restoration site are ideal restoration targets.

The four seed mixes tested in this experiment are representative of two major approaches to post-fire seeding in the region, one utilizing non-native species for soil protection and weed control, and the other focusing on native species with the implicit aim of restoring natural vegetation states. We assessed success in meeting the latter objective by identifying reference communities for the sites and quantifying the degree to which treatments converged on reference community composition. Our findings indicate that native-only seed mixes were superior for restoring toward reference communities compared to conventional mixes containing non-native species, particularly native mixes with higher diversity and higher seeding rates. The failure of conventional mix treatments to transition away from dominance by non-native seeded species should signal caution in the use of these species in situations where restoration objectives extend beyond the narrow set of ecosystem services these species provide. Given the international debate over whether or not to accept or even deliberately introduce non-native species as part of restoration practice (e.g., Jones, 2003; Ewel & Putz, 2004; Hobbs et al., 2009; Belnap et al., 2012; Simberloff & Vitule, 2014; Ramus et al., 2017; Sotka & Byers, 2019), this study provides a template for the kinds of experiments that will assist practitioners in making informed decisions about using vs avoiding non-native species.

AUTHOR CONTRIBUTIONS

FFK and JEO developed the research, building on earlier work by TWT. TWT, DDS, JEO and SLP participated in data collection. JEO analyzed the data with assistance from FFK and wrote the paper with assistance from all authors.

DATA AVAILABILITY STATEMENT

Data and code are available as Appendixes S5 and S6.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1 Precipitation by season and year at study sites

Appendix S2 Arrangement of post-fire seed mix treatments, unburned plots, soils and ecological sites at study sites

Appendix S3 Mean percent cover of species in reference communities and post-fire seeding treatments at Mud Springs site

Appendix S4 Mean percent cover of species in reference communities and post-fire seeding treatments at Jericho site

Appendix S5 CSV file of percent cover data from post-fire treatments and reference communities at study sites

Appendix S6 R scripts for analyses and figures

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